

- of American Foresters national convention, Portland, Oregon. Soc. Am. For., Bethesda, Md.
- RUGGIERO, L. F., AND A. B. CAREY. 1984. A programmatic approach to the study of old-growth forest-wildlife relationships. Pages 340-346 in *New forests for a changing world*, proceedings of the 1983 Society of American Foresters national convention, Portland, Oregon. Soc. Am. For., Bethesda, Md.
- SCHOEN, J. W., M. D. KIRCHOFF, AND O. C. WALLMO. 1984. Sitka black-tailed deer/old-growth relationships in southeast Alaska: implications for management. Pages 315-321 in W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds. *Fish and wildlife relationships in old-growth forests*. Am. Inst. Fish. Res. Biol., Juneau, Alaska.
- , O. C. WALLMO, AND M. D. KIRCHOFF. 1981. Wildlife-forest relationships: is a re-evaluation of old growth necessary? *Trans. North Am. Wildl. and Nat. Resour. Conf.* 46:531-544.
- SIGMAN, M. 1985. Impacts of clear-cut logging in the fish and wildlife resources of southeast Alaska. *Alas. Dep. Fish and Game Tech. Rep.* 85-3. 95pp.
- SIRMON, J. M. 1984. Regional, political and economic issues in managing old growth on national forest land. Pages 325-327 in *New forests for a changing world*, proceedings of the 1983 Society of American Foresters national convention, Portland, Oregon. Soc. Am. For., Bethesda, Md.
- SOCIETY OF AMERICAN FORESTERS. 1984. *Scheduling the harvest of old growth*. Soc. Am. For., Bethesda, Md. 44pp.
- SPIES, T. A., AND J. F. FRANKLIN. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Nat. Areas J.*:In Press.
- TEEGUARDEN, D. E. 1984. National policy, tradeoffs, and issues in managing old-growth forests for multiple benefits. Pages 320-324 in *New forests for a changing world*, proceedings of the 1983 Society of American Foresters national convention, Portland, Oregon. Soc. Am. For., Bethesda, Md.
- THOMAS, J. W., editor. 1979. *Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington*. U.S. Dep. Agric., Agric. Handb. 553. 512pp.
- U.S. FISH AND WILDLIFE SERVICE. 1985. *Endangered species recovery plan: red-cockaded woodpecker (Picoides borealis)*. U.S. Fish and Wildl. Serv., Atlanta, Ga. 88pp.
- WALLMO, O. C., AND J. W. SCHOEN. 1980. Response of deer to secondary forest succession in southeast Alaska. *For. Sci.* 26:448-462.

Received 19 June 1987.

Accepted 30 April 1988.



Wildl. Soc. Bull. 16:262-269, 1988

GRIZZLY BEAR MORTALITY IN THE NORTHERN CONTINENTAL DIVIDE ECOSYSTEM, MONTANA

ROBERT D. BRANNON,¹ *Montana Department of Fish, Wildlife and Parks, FWP Building, Montana State University, Bozeman, MT 59717*

RICHARD D. MACE, *Montana Department of Fish, Wildlife and Parks, P.O. Box 67, Kalispell, MT 59901*

ARNOLD R. DOOD, *Montana Department of Fish, Wildlife and Parks, FWP Building, Montana State University, Bozeman, MT 59717*

The grizzly bear (*Ursus arctos horribilis*) is listed as a threatened species in the lower 48 states of the U.S. (40 Fed. Reg. 31736, 28 Jul 1975). Management of this species, therefore,

is especially important (Peek et al. 1987) and requires accurate information on mortality. Mortality patterns of grizzly and brown bears (*U. a. middendorfi*) have been investigated by Bunnell and Tait (1981, 1985), McCullough (1981), and Knight and Eberhardt (1985). Others have modeled the possible effects of mortality on grizzly bear populations (Bunnell and

¹ Present address: Montana Department of Fish, Wildlife and Parks, 3391 Highway 287, Sheridan, MT 59749.

Tait 1980, Sidorowicz and Gilbert 1981). While the effects of hunting on grizzly bear mortality in Alaska and Canada have been studied (Troyer 1961, Sidorowicz and Gilbert 1981), few data are available on harvest-related mortality of grizzly bears in the lower 48 states.

The Grizzly Bear Recovery Plan (U.S. Fish and Wildl. Serv. 1982a) identified 6 ecosystems for management of grizzly bears in the lower 48 states. The Northern Continental Divide Ecosystem (NCDE) in northwestern Montana contains the largest number of grizzlies of these ecosystems, and is the only one where hunting is allowed. Bunnell and Tait (1980) suggested that quotas on grizzly bear hunting would be an insufficient regulatory device, presumably because of other sources of mortality. In 1975, an annual quota on grizzly bear mortalities from all human causes in the NCDE was established (50 CFR 17.40[b]). Since 1967, data have been collected on mortality of grizzly bears in the NCDE, providing an opportunity to evaluate the effectiveness of a quota in managing grizzly bear mortality. The objectives of our analyses were to document characteristics of grizzly bear mortality, particularly harvest, in the NCDE and to determine the influence of a quota system on those characteristics.

STUDY AREA AND METHODS

The NCDE (Fig. 1) is located in northwestern Montana, where grizzly bears are part of a contiguous population from Montana to Alaska. Grizzly bear mortalities from all causes were recorded annually in the NCDE (K. R. Greer, Mont. Dep. of Fish, Wildl. and Parks, unpubl. data). Data recorded for each death included an identification number, sex, and age; also date, location, and cause of death, if known. Bears were classified as subadults (<5.5 yr old) or adults (≥ 5.5 yr old). Individuals of unknown sex, age, or date of mortality were excluded from analyses.

Mortality of grizzly bears results from hunting, control kills of depredating grizzlies, illegal mortalities including grizzly bears mistakenly killed as black bears, accidental deaths including collisions with trains and automobiles, and kills by natives on Indian Reservation lands.

From 1967 through 1985, there were 2 opening dates for the grizzly bear hunting season in the NCDE. An "early" season in the wilderness portion of the NCDE

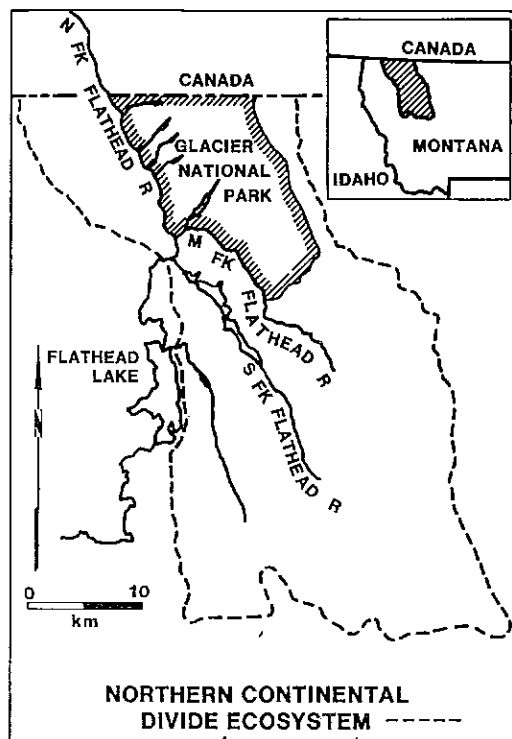


Fig. 1. Location of the Northern Continental Divide Ecosystem in Montana.

began 15 September. The entire NCDE (excluding Glacier Natl. Park) was open for the "general" season from the third week in October to the end of November. These 2 periods are referred to as the early and general seasons. Beginning in 1986, the hunting season opened 1 October.

We used Chi-square analysis to determine the significance of differences in sex and age composition of mortality data. Differences in the mean percent composition by sex, age, and type of mortality before and after the mortality quota of 1975 were tested with the *t*-test after arcsine transformation. We tested variances about these means for equality using an *F'* (folded) statistic (Steel and Torrie 1980). Where variances were determined to be unequal, means were tested using an approximate *t* and Satterthwaite's (1946) approximation to compute degrees of freedom. We used SAS statistical software (SAS Inst. Inc. 1982) for these analyses.

RESULTS

From 1967 through 1986, 445 deaths of bears were recorded. The sex and age class of bears

was known for 414 (Appendix A) and 389 (Appendix B) of these bears, respectively. For bears of known sex, 59% of deaths were males and 41% were females; mortality of males exceeded that of females in 16 of 20 years. Adults constituted 49% and subadults were 51% of the mortalities for which age class was known. Hunting accounted for 54% ($n = 242$) of mortalities ($\bar{x} = 12.1$ bears/yr), and exceeded other causes of death (non-hunting mortality) in 13 of 20 years. Non-hunting mortality accounted for an average of 10.2 bears/year ($n = 203$).

From 1967 through 1986, there was a difference ($\chi^2 = 8.74$, 1 df, $P = 0.003$) in the sex composition of the harvest, but no difference ($\chi^2 = 0.043$, 1 df, $P = 0.84$) in age composition. There was also a difference in the sex composition of non-hunting mortalities ($\chi^2 = 3.93$, 1 df, $P = 0.047$), but no difference ($\chi^2 = 0.80$, 1 df, $P = 0.37$) in the age composition of non-hunting deaths.

The early and general portions of the grizzly bear hunting season accounted for 47.4 and 52.6%, respectively, of the entire season. Using these as expected proportions, analysis of the hunter harvest since 1967 indicated that the proportion of female bears harvested in the early season (62.5%, $n = 60$) and general season (37.5%, $n = 36$) differed ($\chi^2 = 8.78$, 1 df, $P = 0.003$) from that expected.

In 1975, an annual quota of 25 grizzly bear mortalities from all human causes was established for the NCDE. Analyses comparing the sex and age-class (Table 1) composition of mortalities before and after the quota did not indicate any significant differences. Analysis of causes of death before and after the quota (Table 1) indicated some differences. Comparing the annual number of deaths before and after the quota indicated that control and native kills declined by 46 and 95%, respectively, while illegal kills (including mistaken identity) increased by 49% since implementing the quota. Accidental deaths averaged 0.8 bears/year after 1974, but no bears died from accidental human causes before the quota.

Unreported mortalities were defined as mortalities that were not detected or reported. This source of mortality, although difficult to estimate, may be significant. We estimated the extent of this mortality using data from radio-instrumented grizzly bears (C. Servheen, K. Aune, C. Jonkel, R. Mace, unpubl. data). These data included the age, sex, and fate of 84 radio-collared grizzly bears monitored from 1975 through 1986. During this 12-year period, an average of 17.1 bears ($n = 205$ bear/yr) was monitored annually. During the same period an average of 0.5 illegal deaths/year of these bears ($n = 6$) occurred, which would have gone unreported had the bears not been radio-instrumented. Five of these 6 deaths occurred near roads, although the individuals' home ranges included roadless areas and designated wilderness. Using these data, we estimated an annual unreported mortality rate of 2.9%.

DISCUSSION

Since implementation of the annual mortality quota, average annual human-caused mortality of grizzly bears in the NCDE declined by 36%. Hunter harvest was reduced by 38%. Because the annual allowable hunter harvest was adjusted to reflect the number of non-hunting deaths occurring before the hunting season, the reduction in hunter harvest since 1975 is a function of both the mortality quota and the level of non-hunting mortality.

The higher proportion of female harvest during the early grizzly bear hunting season compared to the general season is consistent with other reports (Troyer 1961, Pearson 1975). This higher proportion would be expected because pregnant females and females with cubs generally den earlier than males (Craighead and Craighead 1972, Pearson 1975, Servheen and Klaver 1983), and would not be vulnerable to harvest later in the season.

Since 1975, the female proportion of hunter harvest and total mortality declined by 12 and 13%, respectively, due primarily to a female

Table 1. Comparison of annual reported human-caused mortality of grizzly bears in the Northern Continental Divide Ecosystem, Montana, before (1967–1974) and after (1975–1986) a mortality quota.

Cause of death	Sex/age	Before quota			After quota			P ^a
		\bar{x}	n	Mean %	\bar{x}	n	Mean %	
Hunt	Male	9.0	72	53.8	6.0	72	67.8	0.19
	Female	6.8	54	46.2	3.7	44	32.2	0.19
	Adult	6.3	50	49.1	4.7	56	45.9	0.69
	Subadult	5.5	44	50.9	4.9	59	54.1	0.69
	Total	15.8	126	55.1	9.7	116	52.1	0.54
Nonhunt	Male	4.8	38	47.7	5.1	61	61.8	0.16
	Female	4.3	34	52.3	3.3	39	38.2	0.16
	Adult	4.8	38	52.4	3.8	46	45.1	0.59
	Subadult	5.4	43	47.6	4.4	53	54.9	0.59
	Total	12.6	101	44.9	8.5	102	47.9	0.54
Illegal	Male	0.9	7	69.5	1.8	21	73.6	0.89
	Female	0.5	4	30.5	1.3	16	26.4	0.89
	Adult	1.0	8	50.9	1.5	18	47.7	0.90
	Subadult	1.0	8	49.1	1.6	19	52.3	0.90
	Total	2.4	19	8.4	3.2	38	16.9	0.01
Mistaken identity	Male	0.3	2	85.4	0.5	6	71.8	0.78
	Female	0.1	1	14.6	0.4	5	28.2	0.78
	Adult	0.1	1	14.6	0.5	6	61.2	0.39
	Subadult	0.3	2	85.4	0.4	5	38.8	0.39
	Total	0.4	3	0.3	0.9	11	2.7	0.13
Control	Male	2.6	21	48.6	2.3	28	71.5	0.17
	Female	2.6	21	51.4	1.2	14	28.5	0.17
	Adult	2.5	20	43.8	1.7	20	32.4	0.56
	Subadult	3.0	24	56.2	1.8	21	67.6	0.56
	Total	6.5	52	22.9	3.5	42	17.3	0.41
Accident	Male	0.0	0	0.0	0.4	5	62.9	
	Female	0.0	0	0.0	0.3	4	37.1	
	Adult	0.0	0	0.0	0.2	2	6.7	
	Subadult	0.0	0	0.0	0.6	7	93.3	
	Total	0.0	0	0.0	0.8	9	2.1	0.02
Native	Male	1.0	8	54.0	0.1	1	100.0	0.39
	Female	1.0	8	46.0	0.0	0	0.0	0.39
	Adult	1.1	9	28.9	0.0	0	0.0	0.29
	Subadult	1.1	9	71.1	0.1	1	100.0	0.29
	Total	3.4	27	7.3	0.2	2	0.2	0.02
Total	Male	13.8	110	53.0	11.1	133	62.5	0.13
	Female	11.0	88	47.0	6.9	83	37.5	0.13
	Adult	11.0	88	57.7	8.5	102	46.5	0.34
	Subadult	10.9	87	42.3	9.3	112	53.5	0.34
	Total	28.4	227	100.0	18.2	218	100.0	

^a t-test of difference between mean percentages before (n = 8) and after (n = 12) quota.

mortality subquota of 9 implemented in 1983. Although not statistically significant, we believe that a reduction in the mean female proportion of the hunter harvest (30.3%), control kills (44.6%), all non-hunting mortalities (27.0%), and total mortality (20.2%) is significant to that

population. These declines are due primarily to the total mortality quota and the female mortality subquota. Harvest of cubs or females with cubs has been prohibited since 1947. Beginning in 1985, further protection of young (≤ 2.5 yr old) and females with young has

helped reduce the proportion of females harvested. Females in the hunter harvest may be further reduced by the delayed opening date of 1 October, which began in 1986.

Bunnell and Tait (1985) suggested that the sex ratio of the harvest approaches 1:1 as hunting pressure increases. Because hunters are selective toward males and males are more vulnerable (Pearson 1975, Miller and Ballard 1982, Bunnell and Tait 1985), an even ratio in the harvest further indicates heavy hunting pressure. The sex ratio of hunter-harvested bears since 1975 in the NCDE suggests that hunting pressure on females has not been excessive. The vulnerability of male grizzly bears to hunters probably applies to sources of non-hunting mortality and, in part, explains why more males than females have been killed in control actions and all non-hunting mortality combined.

The quota system has been an effective tool in reducing total female mortality and the female proportion of total mortality. However, the potential exists for mortality data to be skewed toward females without overharvesting them and, at the same time, potentially underharvesting the population. For example, 6 of 9 bears killed in 1987 were females. This level of mortality does not exceed the female subquota, but skews the data toward females. We do not expect this to be a recurring, long-term problem, but emphasize that it is a potential problem with a quota system.

The adoption in 1981 of interagency guidelines for control of problem grizzly bears in the NCDE (U.S. Fish and Wildl. Serv. 1982b) was important in reducing total mortality and the female proportion of mortality. Under these guidelines, bears of any sex or age may cause a depredation problem once without being removed from the population. Females of any age may cause up to 3 problems before being removed from the population.

No hunting regulations have been implemented since 1967 that would be expected to affect the age-class composition of the harvest.

Control guidelines (U.S. Fish and Wildl. Serv. 1982b) adopted in 1981 did not favor either age class, and quotas serve to reduce mortality and the female proportion of mortality, not to affect age composition.

The decline in control kills following the quota is also due to the conservative control guidelines (U.S. Fish and Wildl. Serv. 1982b). The decline in kills by natives is probably more a reflection of the federal listing of the grizzly as threatened than of the mortality quota. The Montana Department of Fish, Wildlife and Parks has no management jurisdiction on Indian Reservation lands.

The increase in illegal mortality after 1974 may be due in part to an increase in reporting of illegal deaths. Of 14 grizzly bear deaths attributed to mistaken identity, 11 occurred since 1975. However, without considering this source of mortality, illegal kills increased by 33%. Some deaths, such as control actions by private citizens, were legal before the federal listing of the grizzly bear in 1975. Since 1975, mistaken identity deaths and control kills by private citizens may have contributed to the increase in illegal mortality. In southern Alberta, hunting of grizzlies was stopped in 1970, after which the number of illegal kills increased. Since 1982, when the hunting season was reopened, illegal kills have declined (L. Russell, Alta. Fish and Wildl. Div., Lethbridge, pers. commun.).

Our estimate of unreported mortality is a first attempt at assessing this source of mortality for grizzly bears in the NCDE and should be viewed accordingly. Because this source of mortality occurs throughout the year, our estimate includes mortality due to crippling by poachers and hunters. The fact that 5 of these 6 deaths occurred near roads suggests that bears are more vulnerable in roaded areas than elsewhere.

All bears in the NCDE are not equally vulnerable to unreported mortality, and vulnerability varies among seasons. Mace et al. (1987)

reported that the age distribution of radio-instrumented bears is skewed toward subadults, because subadults are more vulnerable to capture. Therefore, our estimate of unreported mortality is derived from the most susceptible segment of the population and may constitute an overestimate.

MANAGEMENT IMPLICATIONS

Although Bunnell and Tait (1980) suggested that quota systems would be insufficient to regulate grizzly bear hunter harvest, our analyses indicated that a quota system has been effective in limiting harvest, regulating overall mortality, and controlling mortality of female grizzly bears. However, the same control might be achieved simply through regulation of the harvest and use of the conservative control measures adopted in 1981. One disadvantage of a quota system is that it causes an increase in illegal mortality. Therefore, managers of grizzly bears should carefully consider the advantages and disadvantages of a quota system before implementation. Use of limited-entry permits, as suggested by Bunnell and Tait (1980) will control hunter harvest of grizzly bears, but not non-hunting mortality, and will limit opportunities for hunters. A quota system that limits hunting and legal non-hunting mortality, without limiting hunter opportunity, seems a better means of maintaining hunting.

Regulations are an effective means of controlling hunter harvest of grizzly bears. Implementation of strict regulations on female harvest, including protection of females with young, are effective tools in controlling female harvest. The use of conservative guidelines for controlling depredating bears also limits non-hunting mortality and the female proportion of this mortality.

SUMMARY

We analyzed data on the mortality of 445 grizzly bears in the Northern Continental Di-

vide Ecosystem, Montana, from 1967 through 1986. An average of 22.3 bears/year died from all human causes, 12.1/year by hunter harvest and 10.2/year from causes other than hunting. The sex ratio of bears killed was 59% male and 41% female. In 1975, a quota on annual human-caused grizzly bear mortality was implemented. Since 1975 average annual mortality and hunter harvest declined by 36 and 39%, respectively. The average female proportion of total mortality, hunter harvest, control kills, and all non-hunting mortality declined by 20, 30, 45, and 27%, respectively, since 1975. Annual control kills of depredating grizzlies dropped by 46%, but illegal kills increased by 49% since establishment of the quota. We estimated that unreported mortality occurred at an annual rate of <3%. Our analyses indicated that a quota system, harvest regulations, and depredation control guidelines are effective tools for limiting harvest, total mortality, and female grizzly bear mortality.

Acknowledgments.—Analyses were funded by the Montana Department of Fish, Wildlife and Parks (MDFWP). We would like to thank all the MDFWP personnel who recorded data on grizzly bear mortality. We are particularly grateful to K. R. Greer for his efforts in maintaining the mortality records in 1 location and for compiling the data annually. Without his efforts, this analysis would not have been possible. We also thank the U.S. Fish and Wildlife Service, the U.S. Forest Service, the Bureau of Indian Affairs, and the National Park Service for their cooperation in maintaining mortality records.

LITERATURE CITED

- BUNNELL, F. L., AND D. E. N. TAIT. 1980. Bears in models and in reality—implications to management. *Int. Conf. Bear Res. and Manage.* 4:15–24.
—, AND —. 1981. Population dynamics of bears—implications. Pages 75–98 in C. W. Fowler and T. D. Smith, eds. *Dynamics of large mammal populations*. John Wiley and Sons, New York, N.Y.

Appendix B. Age-class ratios of reported human-caused mortality of grizzly bears in the Northern Continental Divide Ecosystem, Montana, 1967-1986.

Cause of death	Age class	Year																				Total
		67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	
Hunting	Adult	0	1	15	5	8	9	5	7	6	5	2	3	7	9	5	8	2	6	2	1	106
	Subadult	0	4	8	4	5	5	9	9	7	6	3	4	4	2	6	9	5	6	3	4	103
	Unknown	22	4	5	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	33
Illegal	Adult	1	1	0	0	1	2	1	2	4	0	0	2	2	2	2	1	1	2	1	1	26
	Subadult	0	1	1	1	0	3	1	1	2	3	1	2	2	0	0	2	1	3	1	2	27
	Unknown	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
Mistaken identity	Adult	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	2	0	0	0	7
	Subadult	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	2	0	1	0	7
Control	Adult	6	4	3	1	2	3	1	0	0	3	3	1	2	6	0	0	0	1	3	1	40
	Subadult	0	2	4	4	3	6	1	4	1	2	2	1	1	3	3	2	0	1	2	3	45
	Unknown	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	9
Accident	Adult	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	2
	Subadult	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	2	1	7
Native	Adult	0	0	1	0	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	9
	Subadult	0	0	2	0	0	1	1	5	1	0	0	0	0	0	0	0	0	0	0	0	10
	Unknown	4	0	0	0	3	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	10
Total		40	17	39	18	22	30	24	37	22	23	12	13	19	23	17	24	15	20	16	14	445

4

Wildl. Soc. Bull. 16:269-272, 1988

RELATIONSHIP BETWEEN WINTER SEVERITY AND WOLF DEPREDACTIONS ON DOMESTIC ANIMALS IN MINNESOTA

L. DAVID MECH,¹ U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

STEVEN H. FRITTS, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

WILLIAM J. PAUL,² U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

Wolves (*Canis lupus*) prey on domestic animals in Minnesota primarily from May through October, and the extent of depredation varies

considerably from year to year (Fritts 1982). However, no reason for this variation has yet been apparent.

White-tailed deer (*Odocoileus virginianus*) fawns are the primary summer prey of wolves in Minnesota (Frenzel 1974, Van Ballenberghe et al. 1975, Fritts and Mech 1981, Nelson and Mech 1986). Vulnerability of fawns is at least partly a direct function of the previous winter's

¹ Mailing address: North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, MN 55108.

² Mailing address: North Central Experiment Station, University of Minnesota, 1861 East Highway 169, Grand Rapids, MN 55744.